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A SURVEY OF MALE GENITALIA IN LETHAEINE GENERA (HETEROPTERA: LYGAEIDAE: RHYPAROCHROMINAE)

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Abstract.—The clasper and sperm reservoir of 50 species in 31 genera are described, and most are figured. The sperm reservoir, and to a lesser extent the clasper, exhibit a wide variety of form. A preliminary assessment of the taxonomic value of these structures indicates that they are important at several taxonomic levels. These structures are useful in distinguishing externally similar species. Synapomorphies in these structures indicate that some genera are monophyletic, but that other genera are clearly composite and in need of review. Genera are also combined into related groups based on putative apomorphic characters. *Bocundostethus* Scudder, *Kinundastethus* Scudder, and *Microlugenocoris* Scudder are transferred from the Lethaeini to the Antillocorini because they lack synapomorphies characteristic of the Lethaeini.

This study examines characters of the male genitalia, specifically the clasper and sperm reservoir, in the lygaeid tribe Lethaeini (Rhyparochrominae), in order to assess the amount of variation present among genera and species, and to determine the utility of these characters in taxonomic and phylogenetic studies of the tribe. The Lethaeini is an ideal group for a study of this type because the tribe is undoubtedly monophyletic (Ashlock, 1964; Slater and Woodward, 1982), based on the following synapomorphies: linear placement of trichobothria on abdominal sternum five, loss of the y-chromosome, extreme modification of the sperm reservoir, and development of "iridescent" head areas. Out-group comparisons are possible because the sister-group of the Lethaeini has been hypothesized to be the Lilliputocorini; members of both tribes share a reduced dorsal abdominal scent gland in the nymph (Slater and Woodward, 1982). The tribe Antillocorini is the sister-group of the Lethaeini + Lilliputocorini (Slater and Woodward, 1982), providing another out-group.

It became apparent at the outset of this study that 3 African genera described by Scudder (1962) (*Bocundostethus,* with 2 species; *Kinundastethus,* monotypic; and *Microlugenocoris,* monotypic) and placed in the Lethaeini *sensu lato* at that time, actually belong in the related tribe, Antillocorini. They exhibit none of the characteristic lethaeine synapomorphies listed above, and are hereby transferred.

Hemipterists have a long tradition of studying genitalia. In fact, it is particularly appropriate that this paper honor James Slater, since his doctoral thesis was on female genitalia as taxonomic characters in the Miridae (Slater, 1950), and since he has subsequently used both female and male genitalia extensively in his numerous taxonomic studies of the Lygaeidae (see for example Slater, 1979).

While some lygaeid taxonomists have used characters of the entire phallus (Ashlock, 1957, 1964; Harrington, 1980; Malipatil, 1978; Slater, 1985; Sweet, 1967), the present work focuses on just two parts of the phallus, the clasper and the sperm

reservoir. Claspers have traditionally and routinely been used to distinguish between externally very similar species (Slater and O'Donnell, 1979, is just one example), and are generally regarded as species-specific. The sperm reservoir, however, which is the most conspicuous feature of the lethaeine phallus, has been underutilized in taxonomic studies, usually figured incidental to a species or genus description. The comparative approach employed here has been used in other lygaeid subfamilies (Slater, 1979, for the Blissinae, and Slater, 1985, for Australian Lygaeinae), but not yet extensively in the Rhyparochrominae. This first attempt indicates that much taxonomically useful information can be obtained relatively easily.

General morphology of lygaeid male genitalia has been detailed by Bonhag and Wick (1953), Dupuis (1955, 1970), and Ashlock (1957). The following summary deals more specifically with the clasper and sperm reservoir, and with peculiarities of lethaeine genitalia. The claspers and phallus are borne in a cup-like genital capsule (=pygophore) derived from the ninth abdominal segment. The paired symmetrical claspers sit in sockets in the dorsal opening of the capsule. In order to facilitate discussion of the variation among claspers, the following terms are used to designate particular areas of the clasper (Fig. 142).

Blade: the distal curved portion of the clasper; equivalent to "blade" of Ashlock (several papers), Slater and Harrington (1970); and "hook" of Slater and Sweet (1977).

Shank: the basal area of the clasper, between the area of attachment and the blade; equivalent to "shank" of Ashlock (1957) and Slater and Harrington (1970); and "base" of Slater and Sweet (1977).

Area of attachment (Slater and Harrington, 1970): The most basal portion of the shank, where the clasper is attached to the membrane, visible as an opening; equivalent to "basis parameri" of Dupuis (1955) and Ashlock (1957). Frequently a flange (Slater and Sweet, 1977) is present, and the area of attachment is often prolonged laterally.

Inner projection: the projection of the median (relative to insect) curve of the clasper, at the junction of the blade and shank; often with an expanded "mesal" portion that projects "up" from the major plane of the clasper.

Outer projection (Slater and Harrington, 1970): the projection of the outer (relative to insect) curve of the blade, where the expanded basal portion joins the shank. The outer projection is usually broadly rounded in the Lethaeini.

The phallus itself, which appears when inflated as an elongate sheath surrounding a central tube (the endophallus or seminal duct), consists of two parts, a sclerotized phallotheca into which the rest of the phallus fits when not inflated, and the endosoma Ashlock (1957). The endosoma is further divided into a proximal conjunctiva and a distal vesica. The sperm reservoir is located at the proximal end of the vesica and is permanently fixed to its dorsal wall (Ashlock, 1957).

Various authors have used different terms for the structure referred to in this paper as either "sperm reservoir" or "ejaculatory reservoir." The following is a list of equivalent terms: endophallic sperm reservoir (Bonhag and Wick, 1953); conducting chamber (Kumar, 1964); seminal chamber (Sweet, 1967). Dupuis (1955) and Ashlock (1957, 1964) use "ejaculatory reservoir," and Slater and Harrington (1970), Slater and O'Donnell (1978) and several recent authors use "sperm reservoir."

The lethaeine sperm reservoir consists of parts of uncertain homology. Terminology for these parts follows Woodward and O'Donnell (1988), expanding upon initial

attempts by Slater and O'Donnell (1978). The following parts make up the sperm reservoir of lethaeine lygaeids (Figs. 143, 144):

The *conjunctival seminal duct* is that portion of the seminal duct that runs through the lumen of the conjunctiva and into the sperm reservoir. It is equivalent to "ductus seminis conjunctivae" (Ashlock, 1957); "ductus seminis proximalis" (Dupuis, 1970); "the part of the endophallus which leads to the sperm reservoir" (Bonhag and Wick, 1953); and "reservoir duct" (Woodward and Malipatil, 1977), and is undoubtedly homologous across the Lygaeidae.

The *vesical seminal duct* is that portion of the endophallus (seminal duct) which exits the sperm reservoir and continues through the vesica to terminate at the gonopore. It is equivalent to "ductus seminis visicae" (*sic*) (Ashlock, 1957); "ductus seminis distalis" (Dupuis, 1970); "ejaculatory duct" (Slater and O'Donnell, 1978); and "the portion of the endophallus leaving the endophallic sperm reservoir" (Bonhag and Wick, 1953). In lethaeines, the proximal portion of the vesical seminal duct is highly pigmented (=strongly sclerotized) and is treated in this paper as part of the sperm reservoir proper. This part of the vesical seminal duct has been called the "neck" by Ashlock (1957), but since this term has been used to describe what is probably not a homologous structure in other lygaeid sperm reservoirs, it is inappropriate.

The *wings, holding sclerites* and *membranous bulb* are all used in the sense of Ashlock (1957), since each is probably homologous with the structure bearing the same name in other groups.

The *sleeve* is the sclerotized outer wall of the sperm reservoir. It is equivalent to the "sclerotized cylinder" of Slater and O'Donnell (1978), who believed it developed from a basal spur present in other lygaeid sperm reservoirs. I now believe that the sleeve is actually the outer wall of the vesica, which has become sclerotized and rather rigidly associated with the sperm reservoir. The sleeve is often partially surrounded by *corrugations*. Homology of these corrugations is uncertain.

The *arcuate extension* is the curving projection that starts at the insertion of the conjunctival seminal duct and extends to varying degrees around the membranous bulb, often dividing it into two separate lobes. A projection from the opposite side of the opening of the vesical seminal duct may extend outward to meet the arcuate extension. The sleeve connects to the base of the arcuate extension near the conjunctival seminal duct. The arcuate extension has no obvious homolog in other Lygaeidae.

MATERIALS AND METHODS

Fifty species (out of a total of 154 in the Lethaeini) in 31 genera (out of 37 in the Lethaeini) were dissected. Numbers in parentheses after "Species examined" in the Results refer to the number of species studied out of the total number of described species in that genus. In most cases a single individual of each species was dissected. Male genitalia of *Stictolethaeus slateri* O'Donnell are figured in its recent description (O'Donnell, 1991). Males of the following monotypic genera were not available for study: *Carabocoris* Gross, *Lethaeograndellus* Scudder, *Lispolophus* Bergroth, *Orbellis* Distant and *Porrectolethaeus* Scudder. References to original descriptions and subsequent taxonomic changes are given in Slater's (1964) catalog and its forthcoming addendum (Slater and O'Donnell, unpubl.).

Abbreviations in parentheses following locality data refer to the following collections, from which specimens were borrowed: JAS = James A. Slater collection, The University of Connecticut; BM = British Museum (Natural History); QSLD = University of Queensland, Brisbane, Australia.

All observations, dissections and drawings were done with a Leitz-Wetzlar binocular dissecting microscope. Drawings were done at 64× or 160× with the aid of an ocular grid.

Male specimens chosen for dissection were softened for 5–8 minutes in a few drops of relaxing fluid (100 ml absolute ethanol; 75 ml distilled water; 10 ml benzene; 10 ml ethyl acetate). The genital capsule was removed with fine forceps by gently squeezing the abdomen just anterior to the genital capsule. The capsule was placed in a porcelain crucible in a hot solution of 10% potassium hydroxide for clearing. The time necessary to achieve the desired clearing varied with different specimens; to ensure the proper degree of caustic action the capsule was removed to 70% ethanol every 4–5 minutes and checked under the microscope. The specimen was judged sufficiently clear when internal parts of the phallus could be seen through the capsule wall. After clearing, the capsule was transferred in order to the following solutions for three minutes each: glacial acetic acid, distilled water, distilled water (for a second rinse), and 70% ethanol.

The pygophore itself was dissected to study the morphology of the parameres and the sperm reservoir. First, the left clasper was removed using a bent-tipped needle mounted in a wooden matchstick to hook the inner projection. To obtain the sperm reservoir, the entire phallus, including the basal apparatus, was detached from the wall of the capsule and removed through the abdominal opening. The basal apparatus, phallosoma, and membranes were dissected away from the sperm reservoir in that order.

The clasper and sperm reservoir were each transferred in turn to a very small drop of glycerine for drawing. The left clasper of each specimen was drawn from an inner view, as if observing from the center of the capsule looking outward with the clasper *in situ*. In the Lethaeini this offers the best angle for viewing the clasper. Similar orientations were achieved by positioning the area of attachment with the aperture toward the viewer, and the shank as flat against the bottom of the spot plate as possible. Hairs have been omitted from most drawings, for the sake of clarity. The sperm reservoir was drawn in both lateral and dorsal views to convey maximum structural detail. Sclerotized areas are stippled and membranous regions of the bulb, where visible, have been represented by dashed lines.

Dissections were stored in numbered depressions in porcelain spot plates in glycerine. Each dissection was reassociated with the specimen from which it came by

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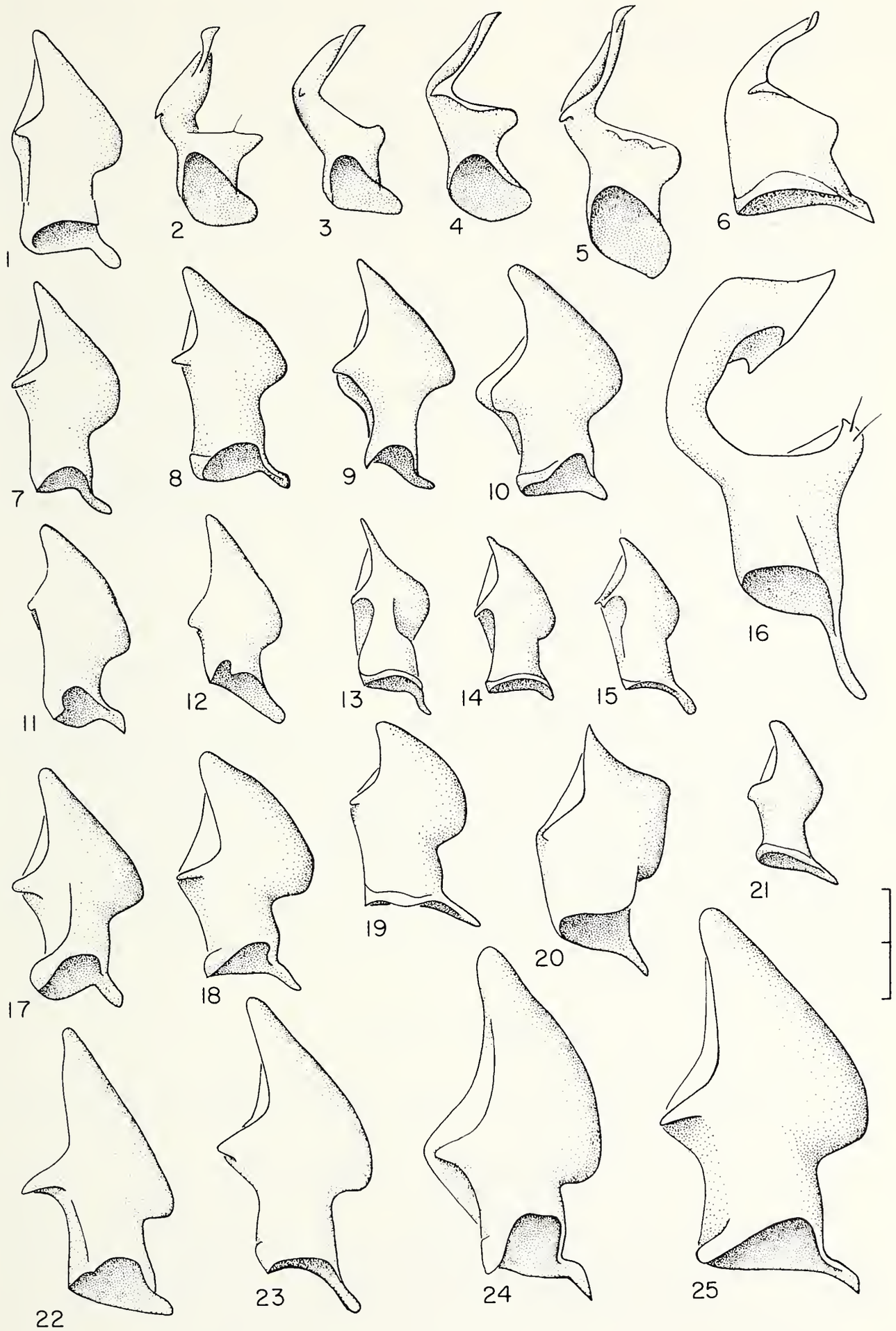
Figs. 1–25. Left paramere, inner view. Scale line = 0.1 mm. 1. *Cryphula trimaculata.* 2. *Paramyocara iridescens.* 3. *Paramyocara punctatum.* 4. *Exomyocara trispinosum.* 5. *Myocara* sp. 6. *Esuris terginus.* 7. *Cryphula affinis.* 8. *Cryphula fasciata.* 9. *Cryphula nitens.* 10. *Rhaptus quadricollis.* 11. *Bubaces* sp. 12. *Coleocoris ocellatus.* 13. *Lampropunctus hirsutus.* 14. *Lamproceps indicus.* 15. *Valtissius distinctus.* 16. *Hexatrichocoris melleus.* 17. *Paragonatas costaricensis.* 18. *Paragonatas divergens.* 19. *Xestocoris nitens.* 20. *Afromydrus slateri.* 21. *Lipostemmata* sp. 22. *Atkinsonianus reticulatus.* 23. *Gonatoides typicus.* 24. *Cistalia signoretti.* 25. *Petissius assimilandus.*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pinning a genitalia vial containing the dissected pieces in glycerine to the same pin as the dissected specimen.

RESULTS: GENITALIC DESCRIPTIONS

Adauctus Distant

Distribution: Oriental.

Species examined (1 of 1): *Adauctus cupreus* Distant: S. India Chikkaballapura, V. Campbell (JAS).

Clasper (Fig. 45): blade tapering to a relatively sharp, recurved point; shank short, twisted; area of attachment not prolonged laterally, without flange; inner projection prominent, acutely pointed, small mesal portion "spur-like"; outer projection broadly rounded, relatively flat.

Sperm reservoir (Figs. 116, 117): vesical seminal duct narrow; sleeve (not apparent) probably fused with vesical seminal duct; arcuate extension moderately sclerotized except around insertion of conjunctival seminal duct where it is heavily sclerotized; arcuate extension broadening distally in dorsal view; shape of membranous bulb unknown; wings and corrugations absent; holding sclerites (not shown in Fig. 117) long, thin, moderately sclerotized and converging distally.

Afromydrus Scudder

Distribution: Ethiopian.

Species examined (1 of 1): *Afromydrus slateri* (Southwood): Nigeria, Ikon CRIN, SE State, 4 April 1975, J. T. Medler (JAS).

Clasper (Fig. 20): blade tapering to a sharp point; shank broad; area of attachment without a flange; inner projection not strongly produced, broadly triangular, with small mesal portion; outer projection large, quadrate, with a rough texture.

Sperm reservoir (Figs. 136, 137): vesical seminal duct with a peculiar septum that divides the opening to the membranous bulb in half (not visible in Fig. 137); sleeve not apparent; arcuate extension ovoid in dorsal view, very flat in lateral view; membranous bulb double but lobes meeting at midline, giving the appearance of a single bulb; corrugations lacking; wings strap-like; holding sclerites moderately sclerotized, meeting distally to form a "v."

Aristaenetus Distant

Distribution: Australian.

Species examined (2 of 2): *Aristaenetus diffinis* (Walker) (type species): Australia,

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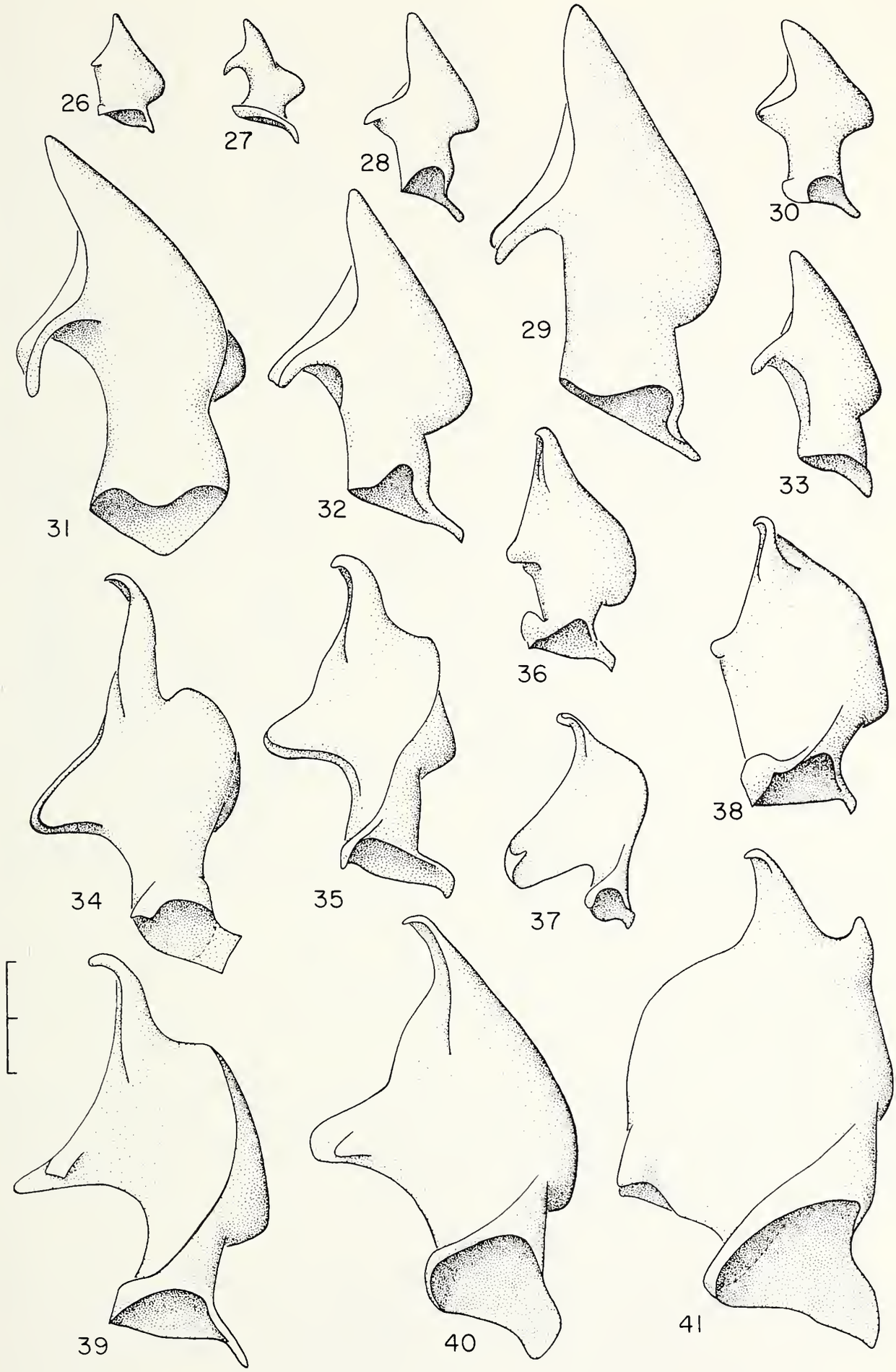
Figs. 26–41. Left paramere, inner view. Scale line = 0.1 mm except for Figs. 36–39 where it equals 0.25 mm. 26. *Ptilocamptocera franzi.* 27. *Camptocera glaberrima.* 28. *Sweetolethaeus macchiaensis.* 29. *Lethaeus longirostris.* 30. *Noteolethaeus armstrongi.* 31. *Lethaeus cribratissimus.* 32. *Lethaeus africanus.* 33. *Lethaeus nitidus.* 34. *Lophoraglius guttulatus.* 35. *Neolethaeus australiensis.* 36. *Neolethaeus aethiopicus.* 37. *Neolethaeus dallasi.* 38. *Neolethaeus giganteus.* 39. *Neolethaeus tenebrosus.* 40. *Aristaenetus diffinis.* 41. *Aristaenetus similis.*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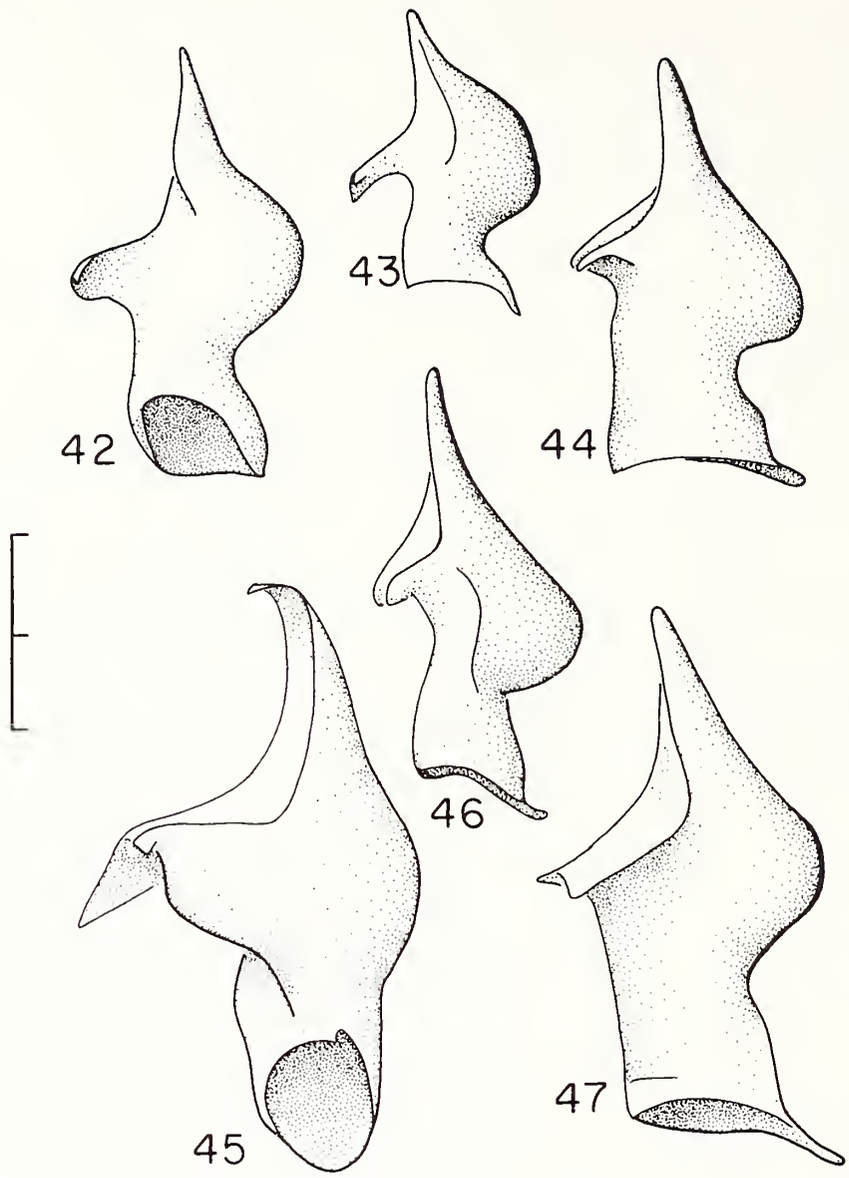

Figs. 42–47. Left paramere, inner view. Scale line = 0.1 mm. 42. *Diniella nitida.* 43. *Diniella laeviuscula.* 44. *Austroxestus australiensis.* 45. *Adauctus cupreus.* 46. *Diniella pallipes.* 47. *Diniella* sp.

Telegraph Xing, Dulhunty River, Cape York Pen., N. Qld., 2–4-vii-1975, G. B. Monteith (QSLD).

Aristaenetus similis Woodward and O'Donnell: Australia, Brisbane, Qld. 20-v-1964, H. A. Rose (QSLD).

Clasper (Figs. 40, 41): blade with apex narrow and curving, base of blade widened, to an extreme degree in *A. similis* (Fig. 41); shank reduced, concave where it meets the well-developed flange; inner and outer projections varying considerably in shape between species (compare Figs. 40, 41).

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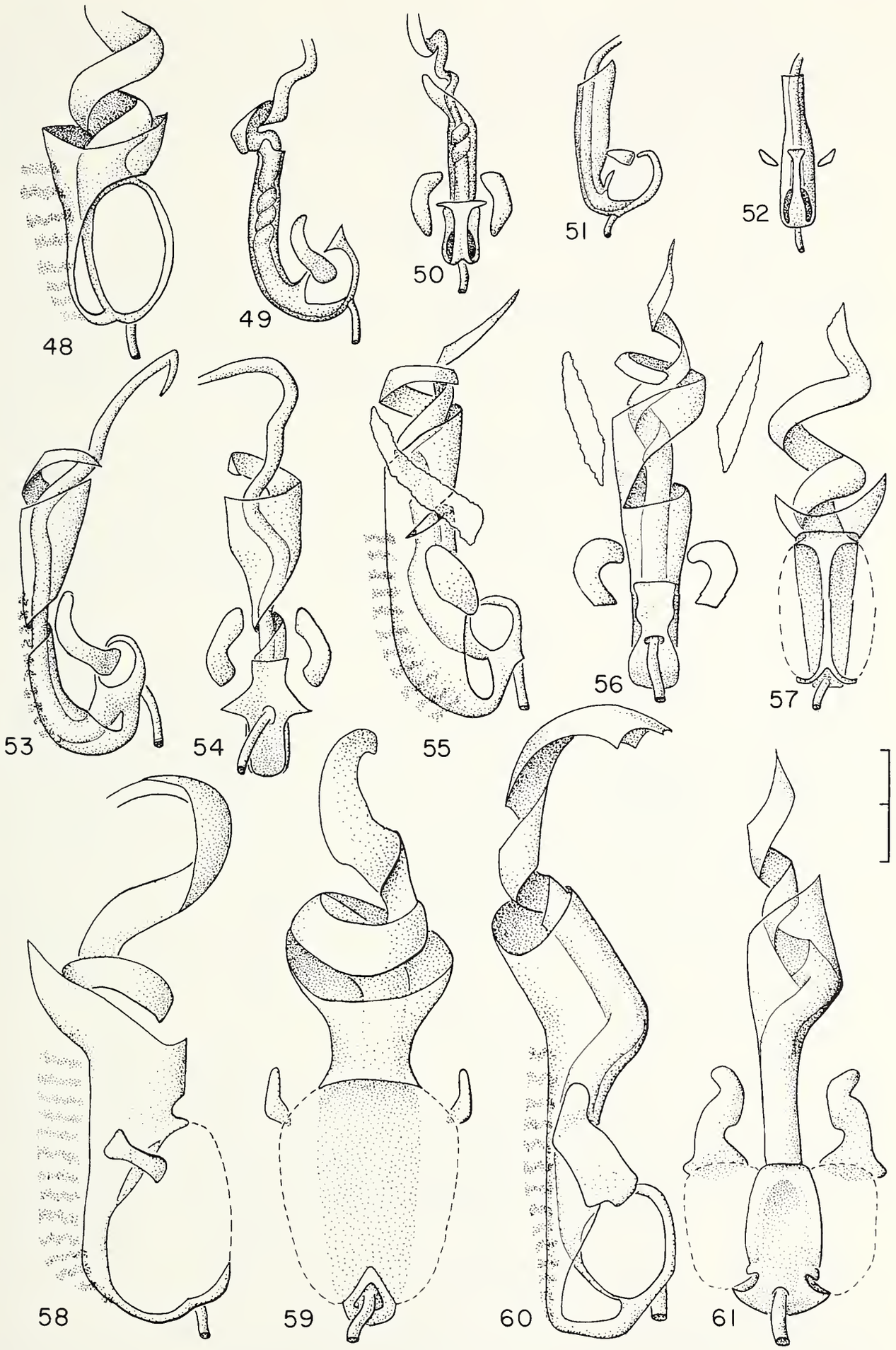
Figs. 48–61. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. Scale line = 0.1 mm. 48. *Paragonatas divergens,* d.v. 49. *Coleocoris ocellatus,* l.v. 50. *Coleocoris ocellatus,* d.v. 51. *Esuris terginus,* l.v. 52. *Esuris terginus,* d.v. 53. *Paragonatas costaricensis,* l.v. 54. *Paragonatas costaricensis,* d.v. 55. *Gonatoides typicus,* l.v. 56. *Gonatoides typicus,* d.v. 57. *Paragonatas divergens,* d.v. 58. *Cistalia signoretii,* l.v. 59. *Cistalia signoretii,* d.v. 60. *Petissius assimilandus,* l.v. 61. *Petissius assimilandus,* d.v.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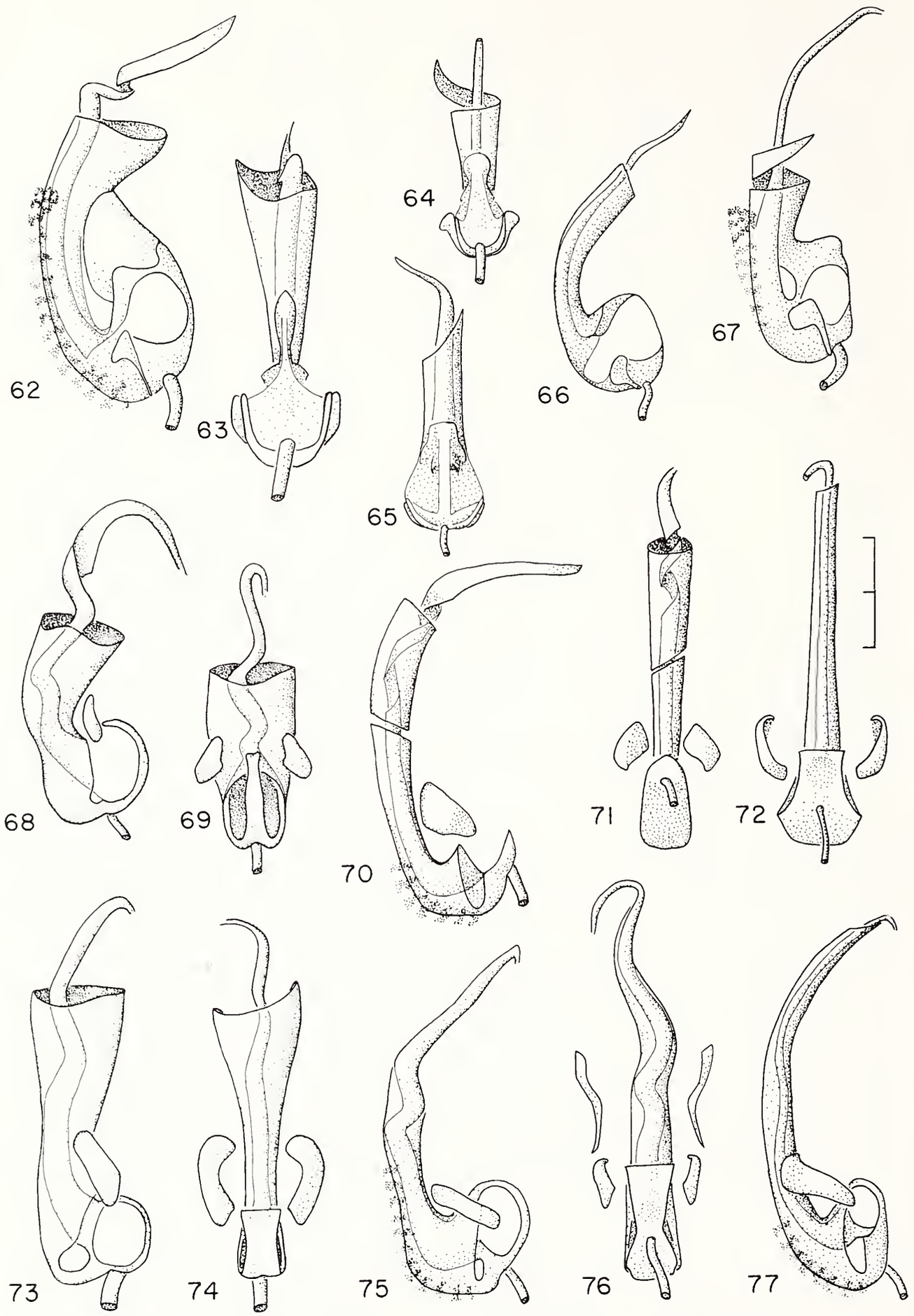

Figs. 62–77. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. (Scale line = 0.1 mm.) 62. *Myocara* sp., l.v. 63. *Myocara* sp., d.v. 64. *Exomyocara trispinosum,* d.v. 65. *Paramyocara punctatum,* d.v. 66. *Paramyocara punctatum,* l.v. 67. *Exomyocara trispinosum,* l.v. 68. *Cryphula*

Sperm reservoir (Figs. 93, 94, 114, 118): vesical seminal duct long, coiled for several turns apically; sleeve moderately sclerotized, fused with vesical seminal duct distally; arcuate extension narrow or broad in dorsal view; shape of membranous bulb uncertain, probably single; wings short and broad; corrugations absent; holding sclerites very long, curving proximally around wings, and meeting distally to form a "v."

Atkinsonianus Distant

Distribution: Oriental.

Species examined (1 of 1): *Atkinsonianus reticulatus* Distant: N. India: Darjeeling 7,000 ft. 11-20-iii-1924, Maj. R. W. G. Hingston (BM).

Clasper (Fig. 22): blade long, apex pointed; area of attachment without a flange; inner projection narrow, pointed; outer projection with long blade portion, relatively acute.

Sperm Reservoir (Figs. 110, 111): vesical seminal duct twisted apically, and surrounded by moderately sclerotized sleeve; arcuate extension meeting an extension of the sleeve midway around the membranous bulb; membranous bulb double, each lobe slightly angled towards vesical seminal duct; wings quadrate; corrugations lacking; holding sclerites form a "v," but extremely faint and barely visible.

Austroxestus Woodward

Distribution: Australian.

Species examined (1 of 5): *Austroxestus australiensis* Woodward: Tasmania, Forth Falls via Sheffield, 5-II-1967, G. Monteith (QSLD).

Clasper (Fig. 44): blade narrow, tapering to a relatively sharp point; shank broad; area of attachment without a flange; inner projection prominent, with small, thin mesal portion; outer projection prominent, relatively acute.

Sperm Reservoir (Figs. 108, 109): Vesical seminal duct surrounded by a lightly sclerotized sleeve; sleeve and vesical seminal duct extending around "top" of membranous bulb to meet arcuate extension; arcuate extension rectangular in dorsal view; membranous bulb double, each lobe quite large (not illustrated); wings, corrugations, and holding sclerites absent.

Bubaces Distant

Distribution: Neotropical.

Species examined (1 of 4): *Bubaces uhleri* (Distant): St. Lucia, BWI, 2 mi N Castries, VI-22-1973, Baranowski, O'Rourke, Picchi, Slater (JAS).

Clasper (Fig. 11): blade considerably longer on outer curvature than on inner curvature; shank short; area of attachment without flange; inner projection small; outer projection relatively sharp.

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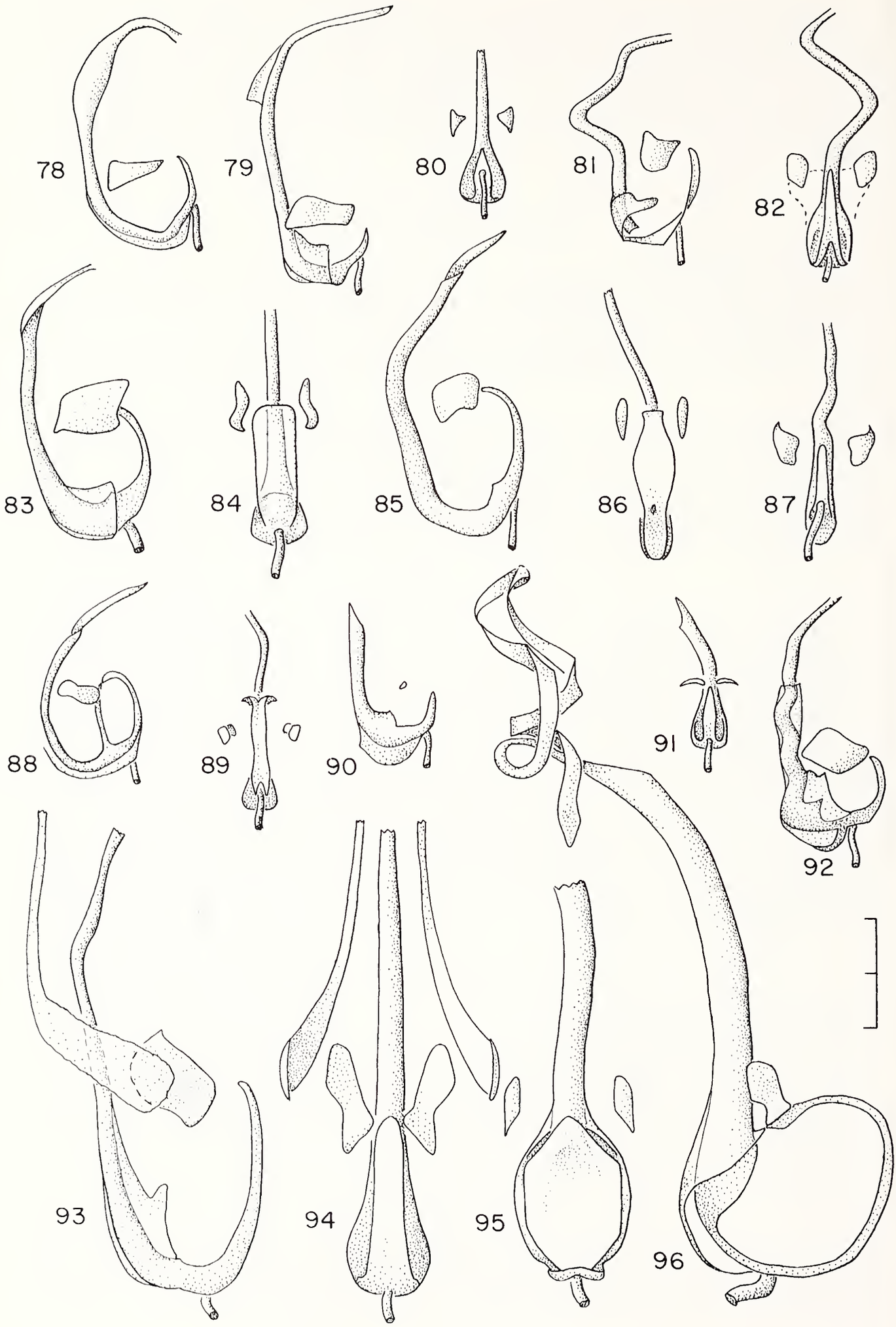
nitens, d.v. 69. *Cryphula nitens,* l.v. 70. *Cryphula affinis,* l.v. 71. *Cryphula affinis,* d.v. 72. *Cryphula fasciata,* d.v. 73. *Rhaptus quadricollis,* l.v. 74. *Rhaptus quadricollis,* d.v. 75. *Cryphula trimaculata,* l.v. 76. *Cryphula trimaculata,* d.v. 77. *Cryphula fasciata,* l.v.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Sperm Reservoir (Figs. 97, 98): vesical seminal duct surrounded by a proximally moderately sclerotized sleeve; sleeve with 2 "arms" that almost enclose conjunctival seminal duct, sleeve also with an extension opposite the arcuate extension; arcuate extension only lightly sclerotized; membranous bulb heart-shaped in dorsal view (not illustrated); wings rectangular, "bent" towards each other; corrugations and holding sclerites lacking.

Camptocera Jakovlev

Distribution: Palearctic, Ethiopian, Oriental.

Species examined (1 of 2); *Camptocera glaberrima* (Walker): Spain Madrid, IV-1909 (JAS).

Clasper (Fig. 27): blade small; shank wide, short; area of attachment with a flange; inner projection prominent, recurved apically; outer projection prominent, triangular, close to area of attachment.

Sperm Reservoir: (Figs. 90, 91): vesical seminal duct not surrounded by a sleeve; sleeve reduced to a heavily sclerotized structure just distal to insertion of conjunctival seminal duct; arcuate extension short, stout but tapering apically in dorsal view; wings narrow, thin, projecting out laterally instead of toward the vesical seminal duct; corrugations and holding sclerites absent.

Cistalia Stål

Distribution: Neotropical, Nearctic.

Species examined (2 of 5): *Cistalia micans* Slater and O'Donnell: Brazil Espiritu Santu: Linhares, Sept. 1972, M. Alvarenga (JAS) (see Slater and O'Donnell, 1978 for figures). *Cistalia signoretii* (Guerin-Meneville) (type species): Brazil Piracicaba S.P. XII-2-1965, C. A. Triplehorn, blacklight trap (JAS).

Clasper (Fig. 24): blade wide, prominent; shank reduced; area of attachment with partially developed flange; inner projection very large, triangular, with mesal portion quite large; outer projection large, meeting shank at a right angle near area of attachment.

Sperm Reservoir (Figs 58, 59): vesical seminal duct flattened and twisted apically; sleeve very prominent, widened distally; arcuate extension small; membranous bulb not bilobed; wings small, rectangular; corrugations heavily sclerotized, very prominent; holding sclerites absent.

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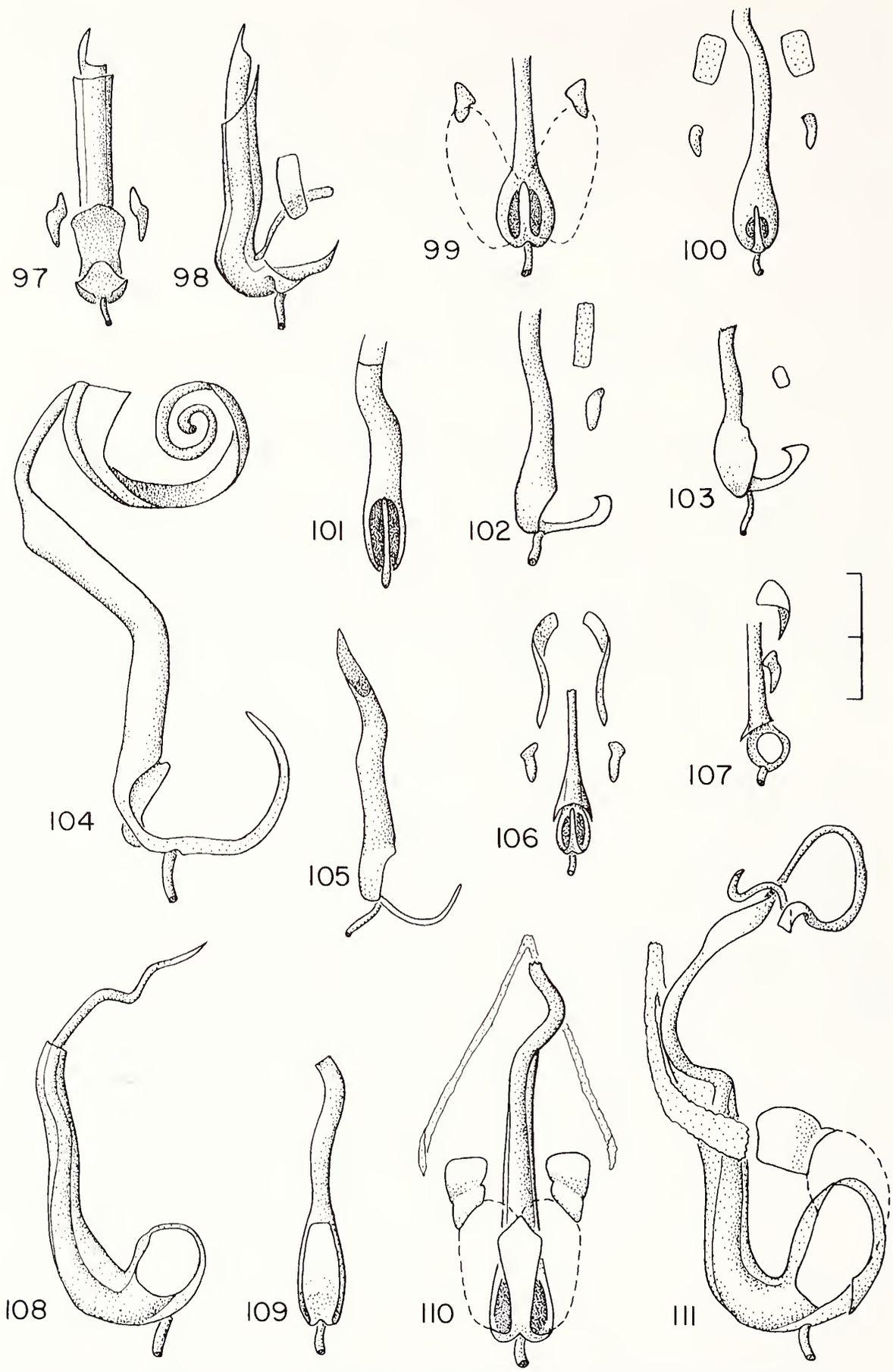
Figs. 78–96. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. Scale line = 0.1 mm. 78. *Lipostemmata* sp., l.v. 79. *Lipostemmata major,* l.v. 80. *Lipostemmata* sp. (same as no. 78), d.v. 81. *Valtissius distinctus,* l.v. 82. *Valtissius distinctus,* d.v. 83. *Lamproceps indicus,* l.v. 84. *Lamproceps indicus,* d.v. 85. *Lampropunctus hirsutus,* l.v. 86. *Lampropunctus hirsutus,* d.v. 87. *Xestocoris nitens,* d.v. 88. *Ptilocamptocera franzi,* l.v. 89. *Ptilocamptocera franzi,* d.v. 90. *Camptocera glaberrima,* l.v. 91. *Camptocera glaberrima,* d.v. 92. *Xestocoris nitens,* d.v. 93. *Aristaenetus diffinis,* l.v. 94. *Aristaenetus diffinis,* d.v. 95. *Hexatrichocoris melleus,* d.v. 96. *Hexatrichocoris melleus,* l.v.



Figs. 97–111. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. (Scale line = 0.1 mm.) 97. *Bubaces* sp., d.v. 98. *Bubaces* sp., l.v. 99. *Diniella laevicollis,* d.v. 100. *Diniella nitida,* l.v. 101. *Diniella pallipes,* d.v. 102. *Diniella nitida,* l.v. 103. *Diniella laevicollis,* l.v. 104. *Diniella* sp., l.v. 105. *Diniella pallipes,* l.v. 106. *Diniella laeviuscula,* d.v. 107. *Diniella laeviuscula,* l.v. 108. *Austroxestus australiensis,* l.v. 109. *Austroxestus australiensis,* d.v. 110. *Atkinsonianus reticulatus,* d.v. 111. *Atkinsonianus reticulatus,* l.v.

Coleocoris Gross

Distribution: Australian.

Species examined (1 of 3): *Coleocoris ocellatus* Gross: W. Australia Torbay 14 mi W Albany, XII-26-1971, J. A. Slater (JAS).

Clasper (Fig. 12): blade triangular, long and pointed; shank relatively short; area of attachment with a prominently "notched" aperture, lacking a flange; mesal portion of inner projection broad and thumb-like; outer projection broadly triangular.

Sperm Reservoir (Figs. 49, 50): vesical seminal duct tightly coiled within sleeve and twisted beyond it; sleeve forming a projection that extends almost to the arcuate extension; arcuate extension well-developed, with an apical protrusion visible in lateral view; membranous bulb with a lobe extending to each wing; wings rectangular; corrugations and holding sclerites lacking.

Cryphula Stål

Distribution: Neotropical, Nearctic.

Species examined (4 of 11): *Cryphula affinis* (Distant): Brazil Piracicaba, S.P., XI-11-1965, C. A. Triplehorn, black light (JAS).

Cryphula fasciata (Distant): Tole Panama Champion (JAS).

Cryphula nitens Barber: California Dune Lakes 3 mi S Oceano, X-11-1974, J. Doyen, stabilized dunes (JAS).

Cryphula trimaculata (Distant): Conn. Barn Island Stonington, VI-9-1976, Slater, O'Donnell, Ford (JAS).

Clasper (Figs. 1, 7, 8, 9): blade thickly pointed; flange present or absent; inner and outer projections at about same level along shank; clasper divided almost equally into shank and blade.

Sperm Reservoir (Figs. 68–72, 75–77): vesical seminal duct bent and/or twisted; sleeve prominent, narrow (except in *C. nitens,* Figs. 68, 69); arcuate extension small (Fig. 70), or forming an incomplete bridge (Fig. 68) or complete bridge (Figs. 75, 77) around membranous bulb; membranous bulb double; wings broad (Figs. 70, 71) or relatively long and slender; corrugations present or absent; holding sclerites present or absent.

Diniella Bergroth

Distribution: Ethiopian, Oriental, Australian.

Species examined (5 of 17): *Diniella laevicollis* (Reuter): S. Africa Kruger Nat. Park, 3 mi. E. Satara Camp, 29 Apr. 68, Nwanedzi River J. A. and S. Slater, M. Sweet, T. Schuh (JAS).

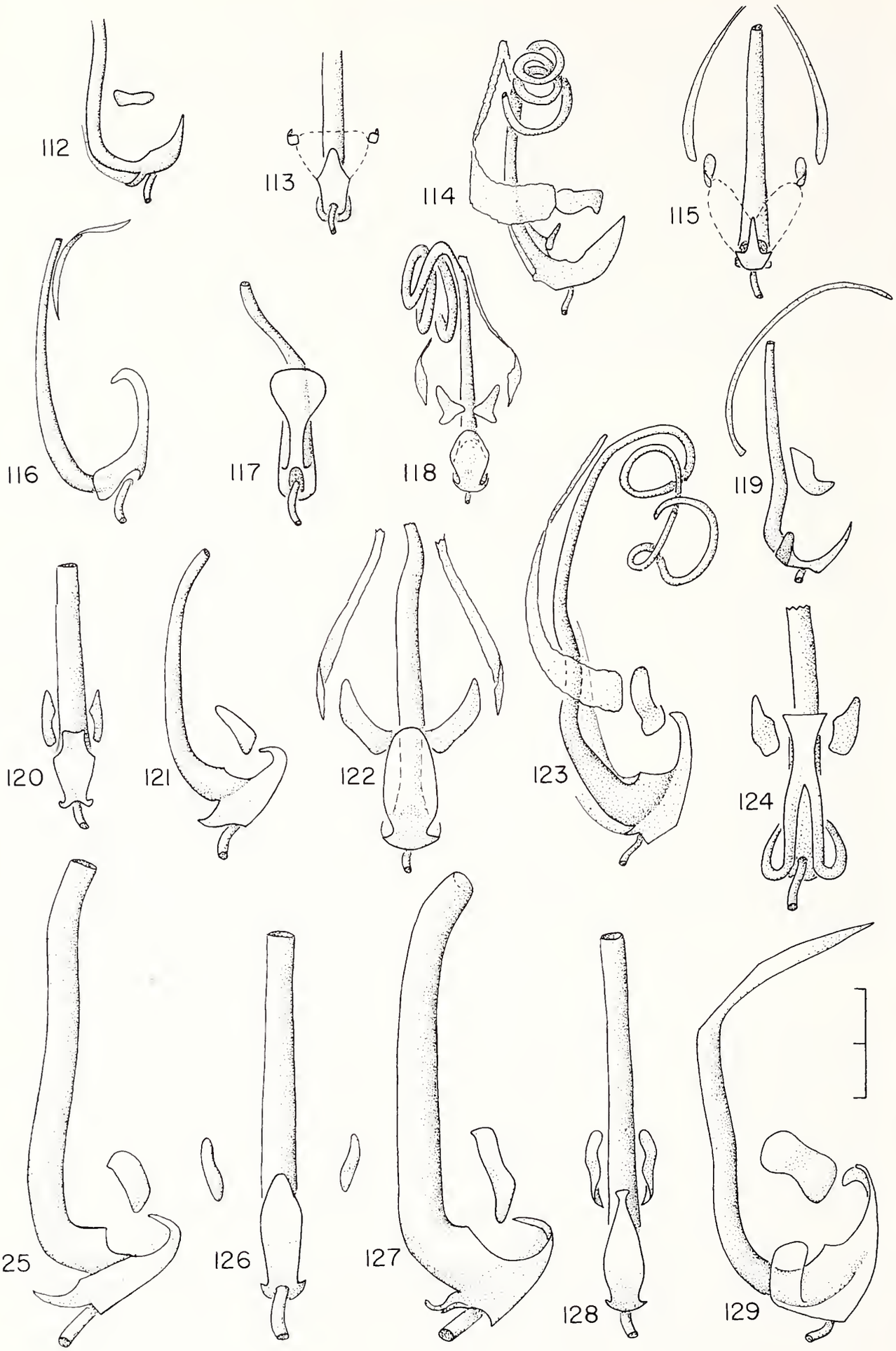
Diniella laeviuscula (Bergroth): Philippines, Luzon, IRRI farm, April 19, 1972, A. D. Pawar (JAS).

Diniella nitida (Reuter): S. Africa Natal Lake, St. Lucia, Charters Creek, Nov. 12, 1967, J. A. and S. Slater, T. Schuh (JAS).

Diniella pallipes (Scott): Shika Is., Fukuoka, X-21-1954, T. Hidaka (JAS).

Diniella sp.: Congo Belge, P.N.U. Kaziba affl. g. Senze S. affl. dr. Lufira (1.140 m.) 4-12-II-1948, Mis G. F. deWitte 1266a (JAS).

Clasper (Figs. 42, 43, 46, 47) (*D. laevicollis* not illustrated): blade slender, tapering to a relatively sharp point; shank broad or slender; area of attachment without a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flange; inner projection variable; outer projection broadly rounded (Figs. 42, 43) or relatively more acute (Fig. 46).

Sperm Reservoir (Figs. 99–107) (*Diniella* sp. not shown in d.v.): vesical seminal duct with sleeve apparent only in *D. laeviuscula* (Figs. 106, 107) and *D.* sp. (Fig. 104); vesical seminal duct otherwise partially or completely fused with sleeve; arcuate extension long, thin in both dorsal and lateral views, curved or straight at apex, and forming a complete bridge in one species, *D. laeviuscula* (Fig. 107); membranous bulb double, lobes large; wings usually small, absent in *D. pallipes*; corrugations lacking; holding sclerites absent (Figs. 101, 105), or lightly sclerotized and of various configurations.

Esuris Stål

Distribution: Neotropical.

Species examined (1 of 1): *Esuris terginus* (Stål): Brazil Nova Teutonia, Santa Catarina 27°11′N, 52°23′W, July 10, 1960, Fritz Plaumann (JAS).

Clasper (Fig. 6): highly modified; blade narrow, arising on the inner side of the clasper and extending laterally in the opposite direction from the usual case; base of blade with a small projection pointing mesally (actually the inner projection); shank broad, somewhat flattened; area of attachment with a flange; outer curvature deeply concave; outer projection a small blunt protrusion.

Sperm Reservoir (Figs. 51, 52): vesical seminal duct surrounded by a moderately sclerotized sleeve; arcuate extension well developed, heavily sclerotized; membranous bulb presumably double; wings rectangular; corrugations and holding sclerites lacking.

Exomyocara Slater and Woodward

Distribution: Australian.

Species examined (1 of 2): *Exomyocara tripinosum* Slater and Woodward (type species): Wildlife reserve 21 mi N Perth, W. Australia, XII-16-1971, J. A. Slater, paratype (JAS).

Clasper (Fig. 4): highly modified, "reversed"; inner projection sharply curved toward outer aspect of clasper, with flared ridge along inner angle; outer projection thumb-like.

Sperm Reservoir (Figs. 64, 67): vesical seminal duct surrounded by a prominent sleeve; sleeve with a "lip" near insertion of vesical seminal duct, and also with a

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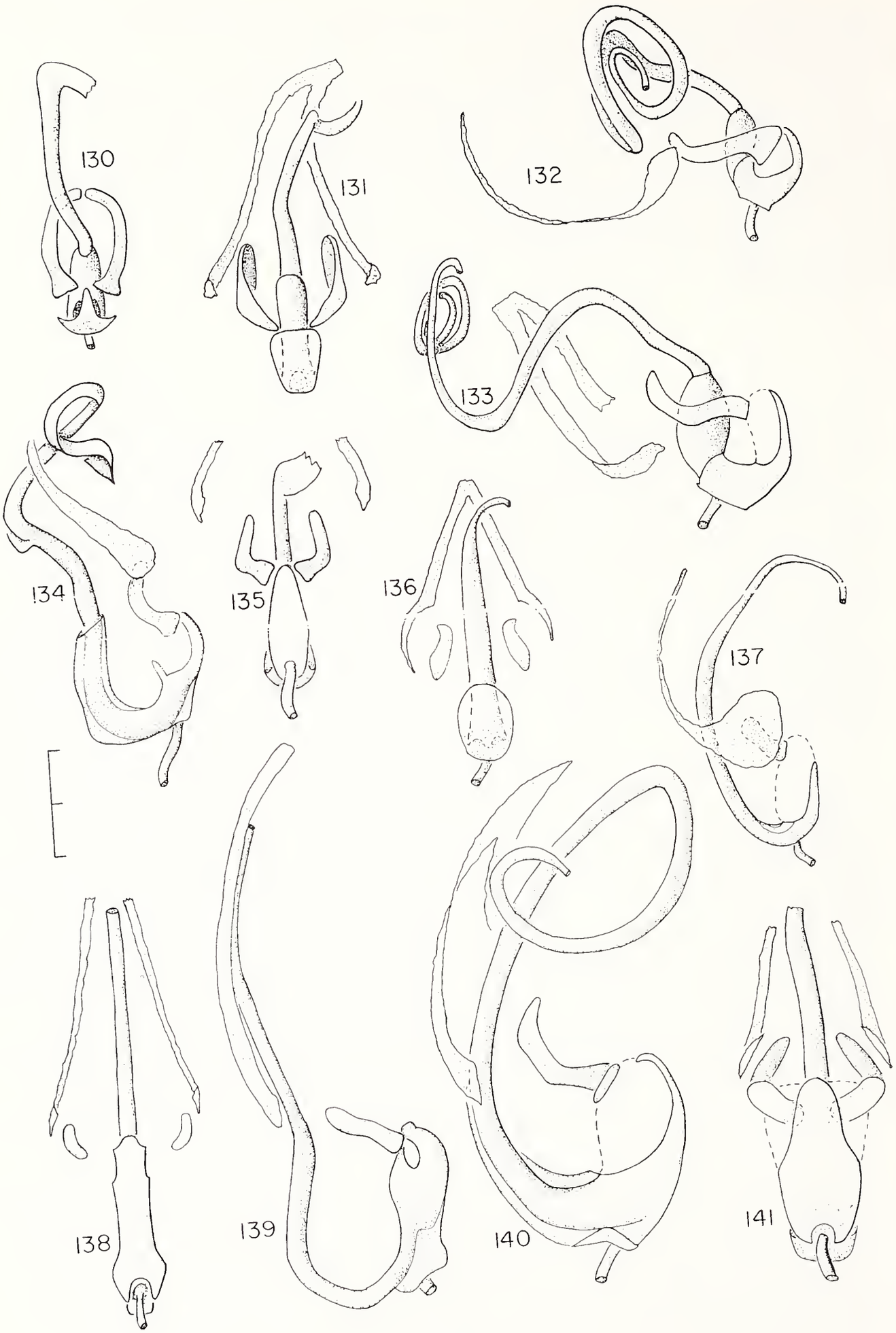
Figs. 112–129. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. Scale line = 0.1 mm except for figures 114 and 118 where it = 0.25 mm. 112. *Noteolethaeus armstrongi*, l.v. 113. *Noteolethaeus armstrongi*, d.v. 114. *Aristaenetus similis*, l.v. 115. *Sweetolethaeus macchiaensis*, d.v. 116. *Adauctus cupreus*, l.v. 117. *Adauctus cupreus*, d.v. 118. *Aristaenetus similis*, d.v. 119. *Sweetolethaeus macchiaensis*, l.v. 120. *Lethaeus nitidus*, d.v. 121. *Lethaeus nitidus*, l.v. 122. *Lophoraglius guttulatus*, d.v. 123. *Lophoraglius guttulatus*, l.v. 124. *Lethaeus africanus*, d.v. 125. *Lethaeus longirostris*, l.v. 126. *Lethaeus longirostris*, d.v. 127. *Lethaeus cribratissimus*, l.v. 128. *Lethaeus cribratissimus*, d.v. 129. *Lethaeus africanus*, l.v.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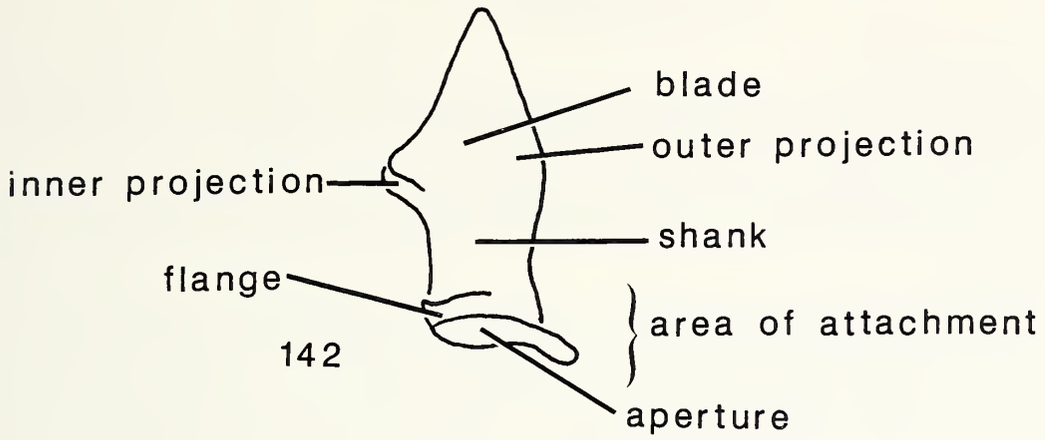

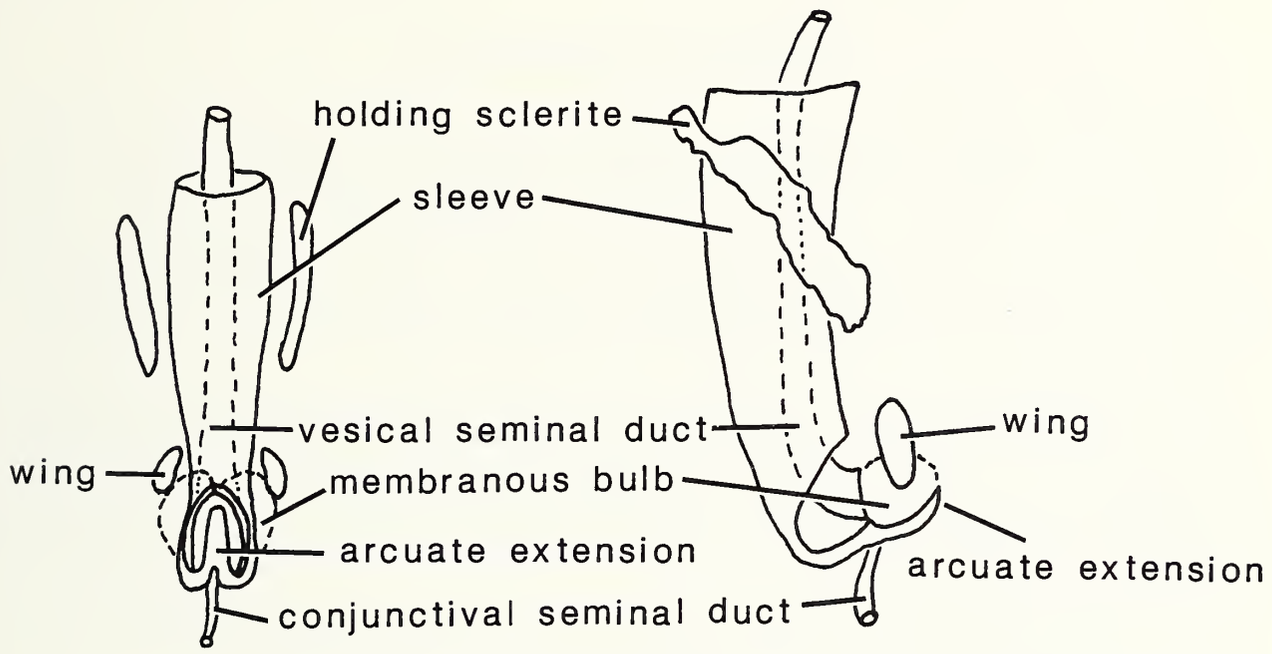

Figs. 142–144. 142. Diagrammatic lethaeine clasper, inner view.143,144. Diagrammatic generalized lethaeine sperm reservoir. 143. Lateral view. 144. Dorsal view.

heavily sclerotized projection dorsally that joins arcuate extension; sleeve ending in an apical twist, arcuate extension only lightly sclerotized; shape of membranous bulb uncertain (presumably similar to *Myocara*); wings and holding sclerites absent; corrugations prominent, especially the distal triangular patch.

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Figs. 130–141. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. Scale line = 0.1 mm except for Figs. 130–133 where it = 0.25 mm. 130. *Neolethaeus aethiopicus,* d.v. 131. *Neolethaeus giganteus,* d.v. 132. *Neolethaeus aethiopicus,* l.v. 133. *Neolethaeus giganteus,* l.v. 134. *Neolethaeus australiensis,* l.v. 135. *Neolethaeus australiensis,* d.v. 136. *Afromydrus slateri,* d.v. 137. *Afromydrus slateri,* l.v. 138. *Neolethaeus tenebrosus,* d.v. 139. *Neolethaeus tenebrosus,* l.v. 140. *Neolethaeus dallasi,* d.v. 141. *Neolethaeus dallasi,* l.v.

Gonatoides Slater

Distribution: Neotropical.

Species examined (1 of 1): *Gonatoides typicus* (Distant): Trinidad: 3 mi E Arima, VI-15-1973, R. Baranowski, F. O'Rourke, V. Picchi, J. Slater (JAS).

Clasper (Fig. 23): Shank broad, tapering to a subacute tip; shank narrower than blade; area of attachment with small partial flange on inner aspect; inner and outer projections prominent.

Sperm Reservoir (Figs. 55, 56): vesical seminal duct twisted and apically "flattened"; sleeve heavily sclerotized, distinct, and helicoid distally; arcuate extension prominent, broad in dorsal view and forming a complete bridge; membranous bulb double, each lobe relatively small; wings thick, curving; corrugations prominent; holding sclerites relatively long, diverging distally.

Hexatrichocoris Kiritshenko

Distribution: Oriental.

Species examined (1 of 1): *Hexatrichocoris melleus* Kiritshenko: Sikkim Tautang 6,000′, IV-24-1924, Maj. R. W. G. Hingston (paratype) (JAS).

Clasper (Fig. 16): highly modified; blade "c-shaped" and extremely large, arising on the mesal side of the clasper and curving outward; apex of blade flattened into a plate (not visible in figure); shank broad, folded longitudinally; area of attachment without a flange; outer projection prominent, thumb-like.

Sperm Reservoir (Figs. 95, 96): vesical seminal duct fused with sleeve except proximally (near insertion of conjunctival seminal duct and where arcuate extension meets the sleeve); vesical seminal duct becoming a "twisted ribbon" apically; arcuate extension wide in dorsal view; membranous bulb double; wings relatively small; corrugations and holding sclerites lacking. The phallus of *Hexatrichocoris melleus* is unusual in the Lethaeini in that 4 (2 pair) large sclerotized spines are present on what I assume to be the conjunctiva (not illustrated). It is unfortunate that their position on the inflated phallus could not be determined.

Lamproceps Reuter

Distribution: Ethiopian, Oriental.

Species examined (1 of 6): *Lamproceps indicus* (Dallas) (type species): Nigeria Lokoja, Kabba, II-24-1949, B. Malkin (JAS).

Clasper (Fig. 14): blade wide, tapering to a sharp point; shank flaring slightly towards base; area of attachment with flange; inner projection triangular, mesal portion small, narrow; outer projection relatively flat.

Sperm Reservoir (Figs. 83, 84): vesical seminal duct twisted apically; sleeve moderately sclerotized, apparent only proximally around vesical seminal duct; arcuate extension long, rectangular in dorsal view; membranous bulb presumably not bilobed; wings quadrate in lateral view; faint corrugations present (not shown in Fig. 83); holding sclerites lacking.

Lampropunctus Scudder

Distribution: Ethiopian.

Species examined (1 of 1): *Lampropunctus hirsutus* Scudder: S. Africa, Transvaal

Zoutpansberg 4,500′, 5 mi N Louis Trichardt, May 6, 1968, J. A. and S. Slater, M. Sweet, and T. Schuh (JAS).

Clasper (Fig. 13): blade narrow, pointed apically; shank "folded"; area of attachment with flange; inner projection triangular, with mesal portion finger-like and not produced extensively; outer curvature with extremely long hairs (not illustrated) on blade portion extending well beyond blade apex; outer projection relatively sharply rounded.

Sperm Reservoir (Figs. 85, 86): vesical seminal duct not surrounded by a sleeve; sleeve fused with vesical seminal duct or lost completely through reduction; arcuate extension long, bulging broadly in dorsal view; membranous bulb appearing bilobed in dorsal view, with each lobe extending to a wing; wings quadrate in lateral view; corrugations and holding sclerites lacking.

Lethaeus Dallas

Distribution: Ethiopian, Palearctic, Oriental.

Species examined (4 of 31): *Lethaeus africanus* Dallas (type species): Nigeria Lokoja Kabba, II-24-49, B. Malkin (JAS).

Lethaeus cribratissimus Stål: Cyprus Polemedia Hills, 600′, II-7-1950, G. Mavrormoustakis (JAS).

Lethaeus longirostris Reuter: Africa: Kenya: Nairobi, K. C., 12-IX-1953, D. C. Thomas (JAS).

Lethaeus nitidus Douglas and Scott: "Cephal Walker," (Greece) (JAS).

Clasper (Figs. 29, 31–33): blade long, tapering to a relatively sharp tip; shank broad, relatively short; area of attachment with lateral extension (except in *Lethaeus cribratissimus,* Fig. 31); inner projection long, finger-like; outer projection only moderately produced.

Sperm Reservoir (Figs. 120, 121, 124–129): vesical seminal duct broad; sleeve apparently reduced to a small spur near insertion of conjunctival seminal duct; conjunctival seminal duct broad in diameter; membranous bulb double, one lobe extending to each wing; wings variable in shape; corrugations and holding sclerites lacking.

Lipostemmata Berg

Distribution: Neotropical.

Species examined (2 of 3): *Lipostemmata major* Ashlock: Paraguay Central Ascuncion, verano, B. Podtiaguin (JAS).

Lipostemmata sp.: Paraguay Central Ascuncion, verano, B. Podtiaguin (JAS).

Clasper (Fig. 21) (*Lipostemmata major* not illustrated): blade relatively wide, tapering apically; shank conventional in illustrated species but expanded just basal to inner projection in *L. major*; area of attachment extending laterally beyond level of of outer projection, with flange; inner projection blunt (Fig. 21) or pointed (not shown); outer projection relatively small.

Sperm Reservoir (Figs. 78–80) (*L. major* not illustrated in d.v.): vesical seminal duct with expanded portion midway to apex; sleeve reduced, fusing with vesical seminal duct distally; arcuate extension short and curving; membranous bulb egg-

shaped, apparently not bilobed; wings rectangular; corrugations and holding sclerites absent.

Lophoraglius Wagner

Distribution: Ethiopian.

Species examined (1 of 8): *L. guttulatus* (Stål): S. Africa Umtentwenti, Natal, VII-1950, A. L. Capener (JAS).

Clasper (Fig. 34): blade relatively slender, pointed, and curving apically; shank narrow; area of attachment with a partial flange, lateral prolongation wide; inner projection large, with large mesal portion; outer projection broadly convex.

Sperm Reservoir (Figs. 122, 123); vesical seminal duct long, coiled distally; sleeve lightly sclerotized, reduced; arcuate extension ovoid in dorsal view; membranous bulb small apparently not double; wings rectangular; corrugations lacking; holding sclerites long, curving towards wings, and meeting distally in a distinct "v."

Myocara Bergroth

Distribution: Australian.

Species examined (1 of 2): *Myocara* sp.: Australia, Parra Wirra Nt. Park near Adelaide, S. Australia, I-5-1972, J. A. Slater (JAS).

Clasper (Fig. 5): highly modified, "reversed"; blade narrow, arising on inner side of clasper, extending laterally towards outer curvature; apex of blade sharply pointed; shank reduced on inner aspect; outer projection blunt, thumb-like, with shelf-like ridge; area of attachment slightly produced laterally, with large aperture and no flange.

Sperm Reservoir (Figs. 62, 63): vesical seminal duct twisted apically, surrounded by a heavily sclerotized sleeve; sleeve with a "lip" near insertion of conjunctival seminal duct; dorsal aspect of sleeve very heavily sclerotized with a projection at the arcuate extension; arcuate extension lightly sclerotized, more visible in lateral view; membranous bulb double, large and quite complex; each lobe extending to the distal end of the sleeve; wings absent, perhaps having fused to form the heavily sclerotized area on the dorsal aspect of the sleeve; holding sclerites absent; corrugations very prominent, with a thickened triangular patch distally.

Neolethaeus Distant

Distribution: Ethiopian, Australian, Oriental.

Species examined (5 of 20): *Neolethaeus aethiopicus* Hesse: Tanzania, Ilonga, IV-14-1965, I. A. D. Robertson, light trap (JAS).

Neolethaeus australiensis Woodward: Australia, McArthur River, N.T. 1-VI-1967, J. Sawdy (JAS).

Neolethaeus dallasi (Scott), Japan Mt. Rokko nr. Kobe, IX-6-1952, E. Nakanishi (JAS).

Neolethaeus giganteus Scudder, Nigeria U-I Campus 1-11-1971, under leaves, Albert V. Oboite (JAS).

Neolethaeus tenebrosus (Distant): Australia Mossman Gorge via Mossman, N. Qld., 25-26-XII-1964, H. A. Rose (JAS).

Clasper (Figs. 35–39): blade slender or broad, but always with curving apex; shank

reduced, often modified by an enlarged flange extending from area of attachment; inner projection varying from relatively small (Figs. 36, 38) to enormously enlarged (Fig. 37) or double (Fig. 39); outer projection prominent, rounded or truncate.

Sperm Reservoir (Figs. 130–135, 138–141), vesical seminal duct long, usually with several apical coils; sleeve apparent (Fig. 134, 140), or partially fused with vesical seminal duct to form a thickened region just distal to opening of vesical seminal duct (Figs. 132, 133) or fused entirely with vesical seminal duct (Fig. 139); arcuate extension varying in dorsal view from small and triangular (Fig. 130) to broad and sub-quadrate (Fig. 131); membranous bulb double, with a tendency to "unite," since lobes are usually quite small; wings long, curving towards vesical seminal duct; corrugations lacking; holding sclerites faint, not forming a "v" (Figs. 134, 135), or prominent, heavily sclerotized and appearing "v-shaped." The considerable variation present in this genus is explored in the Discussion.

Noteolethaeus Woodward and Slater

Distribution: Australian, Ethiopian.

Species examined (1 of 2): *Noteolethaeus armstrongi* Woodward and Slater (type species): Australia, Mt. Coot-tha, Brisbane, Qld., Aug. 9, 1966, R. A. Crowson ex litter (QSLD).

Clasper (Fig. 30): blade triangular, apex bluntly rounded; shank conventional; area of attachment with a wide flange and small aperture; inner projection large, triangular, with small mesal portion; outer projection sharply rounded, meeting blade portion at nearly a right angle.

Sperm Reservoir (Figs. 112, 113): vesical seminal duct heavily sclerotized; sleeve very faint, apparent only ventrally, with a spur present near insertion of conjunctival seminal duct; arcuate extension broad basally, tapering distally, in dorsal view; membranous bulb heart-shaped in dorsal view; wings rectangular, curving toward vesical seminal duct; corrugations and holding sclerites absent.

Paragonatas Barber

Distribution: Neotropical.

Species examined (2 of 2): *Paragonatas costaricensis* (Distant): Panama Maje Station, 90°09′N, 78°47′W, V-17-1975, Engleman, Ramirez, light (JAS).

Paragonatas divergens (Distant) (type species): Dominica 1.5 mi W Rasade, 22-VI-1971, Slater, Baranowski, Harrington (JAS).

Clasper (Figs. 17, 18): blade stout, tapering to a blunt point; shank conventional; area of attachment with an incomplete flange; mesal portion of inner projection short and broad (Fig. 17) or longer and more slender (Fig. 18); outer projection large, prominent.

Sperm Reservoir (Figs. 48, 53, 54, 57): The sperm reservoirs of these two species are quite different and are described separately. See Discussion for further comments.

P. costaricensis (Figs. 53, 54): vesical seminal duct surrounded by a heavily sclerotized, markedly helicoid sleeve; arcuate extension flaring and forming a wide "bridge" across membranous bulb; membranous bulb with 2 small lobes; wings long and slender, very heavily sclerotized; corrugations prominent; holding sclerites lacking.

P. divergens (Figs. 48, 57): vesical seminal duct large in diameter, changing from

a tube to an open "half-tube" as it emerges from the sleeve; sleeve well-developed but short, flaring distally to form a wide opening; arcuate extension narrow and strap-like, continuous with vesical seminal duct; membranous bulb bilobed but lobes not extending laterally; corrugations prominent; wings and holding sclerites lacking.

Paramyocara Woodward and Malipatil

Distribution: Australian, New Zealand.

Species examined (2 of 2): *Paramyocara iridescens* Woodward and Malipatil (type species): Australia, Mt. Carbine, N. Qld., 5-I-1964, G. Montieth (QSLD).

Paramyocara punctatum Woodward and Malipatil: Australia, Brisbane Qld., 22-IV-1969, G. Montieth (QSLD).

Clasper (Figs. 2, 3): highly modified, "reversed" as in *Exomyocara* and *Myocara* (see above); inner projection with hooked apex and small projection at base.

Sperm Reservoir (Figs. 65, 66): vesical seminal duct surrounded by a sleeve; sleeve lipped near insertion of conjunctival seminal duct; dorsal projection of sleeve moderately sclerotized; arcuate extension narrow, very lightly sclerotized, not meeting projection of sleeve; membranous bulb appearing single (a division at midline is visible only when closely examined), not extending much beyond sleeve; wings (contrary to Woodward and Malipatil, 1977) and holding sclerites lacking; corrugations extremely faint, without prominent triangular patch distally.

The sperm reservoir of the type species, *P. iridescens,* is so similar to *Exomyocara trispinosum* that it is not illustrated (see Discussion).

Petissius Distant

Distribution: Neotropical.

Species examined (1 of 3): *Petissius assimilandus* Distant (type species): Panama Las Cumbres, 09°06′N, 79°32′W, XI-13-1973, H. Wolda, light trap (JAS).

Clasper (Fig. 25): broadly triangular; blade tapering to a blunt tip; shank not as large as blade; outer projection prominent; inner projection with small finger-like mesal portion; area of attachment with lateral extension and partial flange.

Sperm Reservoir (Figs. 60, 61): vesical seminal duct large in diameter, with a large bend within the sleeve and two twists beyond it; sclerotized portion of vesical seminal duct ending in two prongs; sleeve strongly sclerotized, close to vesical seminal duct at least proximally, widening distally; arcuate extension forming a continuous bridge; membranous bulb double, each lobe relatively large but not extending beyond bridge of arcuate extension; wings heavily sclerotized, flared where they touch lobes of the bulb; corrugations present but not prominent; holding sclerites lacking.

Ptilocamptocera Wagner

Distribution: Ethiopian.

Species examined (1 of 2): *Ptilocamptocera franzi* Wagner (type species): Nigeria Lokoja Kabba, II-24-1949, B. Malkin (JAS).

Clasper (Fig. 26): blade triangular, tapering to a pointed tip; shank reduced on outer aspect due to large outer projection; area of attachment with incomplete flange;

inner projection triangular with small mesal portion; outer projection relatively acute, joining shank nearly at area of attachment.

Sperm Reservoir (Figs. 88, 89): vesical seminal duct with a prominent twist; sleeve visible ventrally along vesical seminal duct; arcuate extension curving around membranous bulb to meet a projection of the vesical seminal duct; membranous bulb bilobed; wings rectangular; corrugations and holding sclerites lacking.

Rhaptus Stål

Distribution: Neotropical.

Species examined (1 of 1): *Rhaptus quadricollis* (Spinola): Chile Renca Prov. Santiago, VI-1953, L. E. Pena (JAS).

Clasper (Fig. 10): blade broad; shank relatively narrow; area of attachment with flange; inner projection large, bluntly rounded, with mesal portion large and thumb-like; outer projection large, broadly rounded.

Sperm Reservoir (Figs. 73, 74): vesical seminal duct loosely coiled, surrounded by a wide, heavily sclerotized sleeve; conjunctival seminal duct large in diameter; arcuate extension forming a complete bridge; membranous bulb double; wings rectangular, curving towards sleeve; corrugations and holding sclerites absent.

Sweetolethaeus Slater

Distribution: Ethiopian.

Species examined (1 of 2): *Sweetolethaeus macchiaensis* Slater (type species): S. Africa Capetown C.P. Signal Hill, 2,000′, X-5-1974, S. Slater, J. Ecker (JAS).

Clasper (Fig. 28): blade prominent, triangular, apex broadly pointed; shank smaller than blade portion; area of attachment without a flange; inner projection broad, with prominent, finger-like mesal portion; outer projection relatively acute, joining shank at the same level as inner projection.

Sperm Reservoir (Figs. 115, 119): vesical seminal duct not enclosed by a sleeve; sleeve apparently reduced to a thickened "ring" surrounding the opening of the vesical seminal duct; arcuate extension slender; membranous bulb double, lobes large; wings narrow, curving distally; corrugations absent; holding sclerites long, very lightly sclerotized, meeting to form a distinct "v" (distal junction of sclerites not shown in Fig. 115).

Valtissius Barber

Distribution: Nearctic, Neotropical.

Species examined (1 of 3): *Valtissius distinctus* (Distant): Grenada BWI St. George Parish, St. Pauls, VI-18-1973, Baranowski, O'Rourke, Picchi, Slater (JAS).

Clasper (Fig. 15): blade wide, tapering to an acute point; shank extensive; area of attachment with flange; inner projection very broad, produced about as much as broadly rounded outer projection, with small triangular mesal portion.

Sperm Reservoir (Figs. 81, 82): vesical seminal duct with 3 assymetrical twists; sleeve moderately sclerotized, apparent only near opening of vesical seminal duct; arcuate extension long and narrow in dorsal view; membranous bulb bilobed; wings quadrate; corrugations and holding sclerites lacking.

Xestocoris Van Duzee

Distribution: Nearctic, Neotropical.

Species examined (1 of 2): *Xestocoris nitens* Van Duzee: Conn. Mansfield Center, IV-19-1956, J. A. Slater (JAS).

Clasper (Fig.19): blade very wide, tapering to a blunt point; shank broad; area of attachment with flange; inner projection triangular but not strongly produced, mesal portion small, finger-like; outer projection large, broadly and convexly rounded.

Sperm Reservoir (Figs. 87, 92): vesical seminal duct with several bends; sleeve lightly sclerotized proximally except for a "spur" near insertion of conjunctival seminal duct, moderately sclerotized distally where it is tightly appressed to the seminal duct; arcuate extension long and slender in dorsal view; membranous bulb double, each lobe extending to a wing; wings quadrate; corrugations and holding sclerites absent.

DISCUSSION

Lethaeine sperm reservoirs, and to a lesser degree claspers, exhibit a wide variety of form. While many genera exhibit a characteristic sperm reservoir morphology, several genera are so variable that their monophyly is in question. Obviously, more species and type species, and other characters, need to be examined before formal taxonomic changes at the generic level are proposed. It is clear, however, that both the clasper and sperm reservoir offer great potential not only for distinguishing among species, but also for grouping species into monophyletic genera and for combining genera into related groups.

The clasper is relatively less complex than the sperm reservoir, and is less informative phylogenetically. Most lethaeines have claspers that are stout and broadly triangular, with inner and outer projections about equally produced. This is likely to be the plesiomorphic condition, since it is present not only in the Lethaeini, but in the out-groups as well. Several departures from this basic shape represent apomorphic states.

The first of these is the "reversed" clasper shape found in species of *Esuris* (Fig. 6), *Hexatrichocoris* (Fig. 16), *Exomyocara* (Fig. 4), *Myocara* (Fig. 5), and *Paramyocara* (Figs. 2, 3). All of these claspers share the apomorphy of the blade arising on the inner side of the clasper instead of on the outer side, but differences in the areas of attachment, blade and outer projection, as well as differences in the sperm reservoir, indicate that this condition arose three times independently: once in *Esuris,* once in *Hexatrichocoris,* and once in the lineage comprising *Exomyocara, Myocara,* and *Paramyocara.* This peculiar reversed condition also appears to have evolved independently in *Terenocoris nitidus* Slater, an antillocorine.

The second apomorphic clasper shape characterizes all species of *Lethaeus* examined in this study. These claspers (Figs. 29, 31–33) have a long blade, no flange at the area of attachment, and a prominent finger-like inner projection that is strongly deflected toward the base of the clasper.

The genera *Aristaenetus, Lophoraglius,* and *Neolethaeus* form a distinct group based on claspers with an apomorphic shape. Claspers of species in these genera have relatively slender, sickle-shaped blades that curve apically and end in a point (Figs. 34–41). The area of attachment has a prominent flange that imparts a strong concavity

to the inner face of the clasper. The inner projection takes on various modified shapes also. Yet another clearly distinct group consists of species of *Lamproceps, Lampropunctus* and *Valtissius.* These claspers (Figs. 13–15) have apically pointed blades and a small pointed inner projection.

The sperm reservoir is a more complex structure than the clasper. As such, similarity of sperm reservoir morphology is more likely to be synapomorphous and less likely to be homoplasious than is similarity of clasper shape, assuming that at least some of the complex features are apomorphic. Deciding on the plesiomorphic condition, however, is difficult because homologies are uncertain. Based on out-group comparison, my working hypotheses is that a sperm reservoir with most or all of the parts shown in Figures 143 and 144 is closest to the ancestral condition, and that modification of the sperm reservoir has proceeded largely through fusion, reduction or loss of various components.

Like the clasper, the sperm reservoir offers useful characters for recognizing and distinguishing among species. More importantly, many genera have a characteristic sperm reservoir shape, and are thus probably monophyletic. For example, all four species of *Lethaeus* (Figs. 120, 121, 124–129) examined have very similar sperm reservoirs that are unlike other Lethaeini. The complete lack of holding sclerites and the characteristic shape are strong apomorphic characters uniting these species. The type species, *L. africanus,* differs only slightly from the rest of the genus in that the "spur" near the insertion of the conjunctival seminal duct has enlarged to form a pair of flat plates, one on each side of the vesical seminal duct. Presumably the *Lethaeus* type of sperm reservoir has resulted from an extreme reduction of the sleeve, perhaps through an intermediate condition similar to that found in the sperm reservoir of *Noteolethaeus,* which also has a basal "spur" that is perhaps homologous to the one found in *Lethaeus.* This spur may also be homologous with one found in *Xestocoris,* although I have tentatively placed *Xestocoris* with other genera (Group IV below) based on the shape of the wings.

Another example of a genus with a distinct sperm reservoir is *Diniella,* with species united by possessing a fused sleeve and vesical seminal duct. In the sperm reservoir of *D. laeviuscula* (Figs. 106, 107), and *D.* sp. (Fig. 104), this fusion is incomplete. Only about one-fourth of the total number of species in the genus were studied, however.

Several genera, on the other hand, appear composite based on morphology of the sperm reservoir. One such genus is *Neolethaeus.* The three types of sperm reservoirs found in *Neolethaeus* are as different from each other as are the sperm reservoirs of most lethaeine genera. *Neolethaeus aethiopicus* (Figs. 130, 132) and *N. giganteus* (Figs. 131, 133), two African species, have a distinctive synapomorphy in a wide thickened ring or bulge just distal to the opening of the vesical seminal duct (Figs. 132, 133). Undoubtedly these two species are closely related. *Neolethaeus dallasi* (Figs. 140, 141) from Japan, and *N. australiensis* (Figs. 134, 135) lack this thickened ring, and may be more closely related to species in other genera. *Neolethaeus tenebrosus* (Figs. 138, 139) is distinct from the other two types mentioned above, but does not share its distinct morphology with any other species examined thus far.

The two species of *Paragonatas, P. divergens,* the type species (Figs. 48, 57), and *P. costaricensis* (Figs. 53, 54), also have very dissimilar sperm reservoirs. Likewise, the genus *Cryphula* (Figs. 68–72, 75–77) also seems to be composed of two distinct

sperm reservoir types. *Cryphula nitens* (Figs. 68, 69) represents one type, where the sleeve is widely separated from the vesical seminal duct. Another type of sperm reservoir, characterized by prominent corrugations and a sleeve more closely associated with the vesical seminal duct, occurs in the other *Cryphula* species examined (Figs. 70, 71, 75–77). Each of these types also occurs in other Group I genera (see below).

Genera can nevertheless be united into four monophyletic groups based on apomorphic sperm reservoir morphology. The first of these groups, Group I, consists of the following genera: *Cistalia* (Figs. 58, 59), *Coleocoris* (Figs. 49, 50), *Cryphula* (Figs. 68–72, 75–77), *Esuris* (Figs. 51, 52), *Gonatoides* (Figs. 55, 56), *Paragonatas* (Figs. 48, 53, 54, 57), *Petissius* (Figs. 60, 61), and *Rhaptus* (Figs. 73, 74). This group contains species with sperm reservoirs that retain most of the parts shown in Figures 143 and 144. However, if my above hypothesis of character transformation through consolidation and reduction is correct, this group may simply be a phenetic one, based on symplesiomorphy.

Group II genera are characterized by apomorphic, long, v-shaped holding sclerites, and include *Adauctus* (Figs. 116, 117), *Afromydrus* (Figs. 136, 137), *Aristaenetus* (Figs. 93, 94, 114, 118), *Atkinsonianus* (Figs. 110, 111), *Lophoraglius* (Figs. 122, 123), *Neolethaeus* (Figs. 130–135, 138–141), and *Sweetolethaeus* (Figs. 115, 119). Within this sperm reservoir group, *Aristaenetus, Lophoraglius,* and *Neolethaeus* possess claspers of highly modified shapes. It is likely that these three genera shared a common ancestor.

Sperm reservoir Group III comprises the three endemic Australian genera *Exomyocara* (Figs. 64, 67), *Myocara* (Figs. 62, 63), and *Paramyocara* (Figs. 65, 66), and the Neotropical genus *Bubaces* (Figs. 97, 98). The feature that unites these geographically distant genera is the presence of an unusual curled "lip" at the base of the sleeve near the insertion of the conjunctival seminal duct. This lip is greatly expanded in the three Australian genera, giving them their characteristic appearance. The wings may have fused or been otherwise incorporated with the large, heavily sclerotized dorsal structure adjacent to the sleeve that is prominent in all species of this group except *P. punctatum.* Generic limits of the Australian taxa merit review, however, based on examination of the male genitalia. The species of these 3 genera differ from each other as little as do many congeneric species in the Lethaeini, but, more importantly, the sperm reservoir of *Paramyocara iridescens,* the type species, shares the presumed apomorphy of the heavy triangular patch of corrugations with a species of *Exomyocara* (Fig. 67).

The wide, plate-like wings, reduced nature of the sleeve, lack of holding sclerites and overall similarity of shape all seem to indicate a common derivation for Group IV, containing the following genera: *Lamproceps* (Figs. 83, 84), *Lampropunctus* (Figs. 85, 86), *Ptilocamptocera* (Figs. 88, 89), *Valtissius* (Figs. 81, 82) and *Xestocoris* (Figs. 87, 92). *Xestocoris* is enigmatic in that a spur, similar to that found in *Lethaeus* (Figs. 120, 121, 124–129) and *Noteolethaeus* (Figs. 112, 113), is present near the insertion of the conjunctival seminal duct. If this spur proves to be homologous across these taxa, *Lethaeus* and *Noteolethaeus* will be included in Group IV.

Several genera could not be placed in one of the above groups. They are *Austroxestus* (Figs. 108, 109), *Camptocera* (Figs. 90, 91), *Diniella* (Figs. 99–107), *Hexatrichocoris* (Figs. 95, 96), and *Stictolethaeus* (see O'Donnell, 1991).

The clasper and sperm reservoir provide valuable taxonomic characters to distinguish between species, to define monophyletic genera, and to establish sister-group relationships among genera. Difficulties in interpretation of homology and in polarization of character states may be overcome eventually by examining more taxa. It is clear that male genitalia have much to contribute to refining the classification of the Lethaeini.

LITERATURE CITED

Ashlock, P. D. 1957. An investigation of the taxonomic value of the phallus in the Lygaeidae (Hemiptera-Heteroptera). Ann. Entomol. Soc. Amer. 50:407–426.

Ashlock, P. D. 1964. Two new tribes of Rhyparochrominae: A re-evaluation of the Lethaeini (Hemiptera-Heteroptera: Lygaeidae). Ann. Entomol. Soc. Amer. 57:414–422.

Bonhag, P. F., and J. R. Wick. 1953. The functional anatomy of the male and female reproductive systems of the milkweed bug, *Oncopeltus fasciatus* (Dallas) (Heteroptera, Lygaeidae). J. Morph. 93:177–284.

Dupuis, C. 1955. Les genitalia des Hemipteres Heteropters (Genitalia externes des deux sexes; voies ectodermiques femelles). Paris Mus. d'Hist. Nat. Mem., Ser. A. (n.s.) 6:183–278.

Dupuis, C. 1970. Heteroptera. Pages 190–209 *in*: S. L. Tuxen (ed.), Taxonomists' Glossary of Genitalia in Insects. 2nd Ed. Munksgaard, Copenhagen, 359 pp.

Harrington, B. J. 1980. A generic level revision and cladistic analysis of the Myodochini of the World (Hemiptera, Lygaeidae, Rhyparochrominae) Bull. Am. Mus. Nat. Hist. 167: 45–116.

Kumar, R. 1964. On the structure and function of the so-called ejaculatory reservoir in Pentatomoidea (Hemiptera: Heteroptera). Proc. Roy. Soc. Queensland 75:51–65.

Malipatil, M. B. 1978. Revision of the Myodochini (Hemiptera: Lygaeidae: Rhyparochrominae) of the Australian Region. Austr. Jour. Zoo. Suppl. Ser. No. 56:1–178.

O'Donnell, J. E. 1991. A new coleopteroid lethaeine from southern South America Hemiptera: Lygaeidae: Rhyparochrominae) J. New York Entom. Soc. 99:87–96.

Scudder G. G. E. 1962. Resultats scientifiques des missions zoologiques de L'I.R.S.A.C. en Afrique orientale (P. Basilewsky et N. Leleup, 1957) LXXXIII. Hemiptera Lygaeidae. Mus. Roy. Afr. Centr. Sci. Zool. N. 110:400–453.

Slater, A. 1985. A taxonomic revision of the Lygaeinae of Australia (Heteroptera: Lygaeidae) Univ. of Kansas Sci. Bull. 52(8):301–481.

Slater, J. A. 1950. An investigation of the female genitalia as taxonomic characters on the Miridae (Hemiptera). Iowa State College J. Sci. 25:1–81.

Slater, J. A. 1964. A catalogue of the Lygaeidae of the world. 2 vol. The University of Connecticut, Storrs, 1668 pp.

Slater, J. A. 1979. The systematics, phylogeny and zoogeography of the Blissinae of the World (Hemiptera, Lygaeidae). Bull. Amer. Mus. Nat. Hist. 165:1–180.

Slater, J. A. and J. E. Harrington. 1970. A revision of the genus *Ischnodemus* Fieber in the Ethiopian region (Hemiptera: Lygaeidae, Blissinae). Ann. Transvaal Museum 26:211–279.

Slater, J. A. and J. E. O'Donnell. 1978. A new species of *Cistalia* from Brazil and comments on systematic characters in the Lethaeini (Hemiptera: Lygaeidae). Fla. Ent. 61:49–55.

Slater, J. A. and J. E. O'Donnell. 1979. Analysis of the *Ozophora laticephala*-complex with the description of eight new species (Hemiptera: Lygaeidae). J. Kansas Entomol. Soc. 52:154–179.

Slater, J. A. and M. H. Sweet. 1977. The genus Plinthisus in the Australian region (Hemiptera: Lygaeidae). Entomol. Scand. 8: 109–152.

Slater, J. A. and T. E. Woodward. 1982. Lilliputocorini, a new tribe with six new species of *Lilliputocoris,* and a cladistic analysis of the Rhyparochrominae (Hemiptera, Lygaeidae). Am. Mus. Novitates 2754:1–23.

Sweet, M. H. 1967. The tribal classification of the Rhyparochrominae (Heteroptera: Lygaeidae). Ann. Entomol. Soc. Amer. 60:208–226.

Woodward, T. E. and M. B. Malipatil. 1977. A new genus and two new species of Lethaeini (Hemiptera: Lygaeidae: Rhyparochrominae). J. Aust. Entomol. Soc. 16:341–346.

Woodward, T. E. and J. E. O'Donnell. 1988. The genus *Aristaenetus* Distant (Hemiptera: Lygaeidae: Rhyparochrominae) with the description of a new species. Memoirs of the Queensland Museum 25:481–491.

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